

SEASONAL SPAWNING OF SERGEANT MAJOR DAMSELFISH *ABUDEFDUF VAIGIENSIS* IN THE SUBTROPICAL WATERS OF TAIWAN¹

RONG-QUEN JAN² and RUPERT F.G. ORMOND³

²*Institute of Zoology, Academia Sinica, Nankang, Taipei, Taiwan 11529,
Republic of China*

and

³*Department of Biology, University of York, YO1 5DD, U.K.*

(Accepted March 20, 1992)

Rong-Quen Jan and Rupert F.G. Ormond (1992) Seasonal spawning of sergeant major damselfish *Abudefduf vaigiensis* in the subtropical waters of Taiwan. Bull. Inst. Zool. Academia Sinica 31(4): 290-311. A survey of the spawning activity of the sergeant major damselfish, *Abudefduf vaigiensis*, was undertaken off the northern coast of Taiwan (121°41'E, 25°12'N) from April to October, 1986. Temporal variation in spawning intensity and its correlation with environmental factors were analyzed. Spawning was observed in 58 of the 169 days between May 1 (the date on which the first nests were found) and October 16 (the date the last nests were found). In total, 966 nests were located during this period. Spawning occurred in the warm season of the year, but the correlation between daily spawning intensity (assessed as number of new nests found) and water temperature was not significant. Within the spawning period, peak spawning occurred twice, once in May and again in July. We found no indication of a significant lunar component or long-term periodicity in spawning activity within the spawning period. We did find that the spawning period was highly correlated with higher zooplankton production. Though the overall spawning period occurred entirely within the typhoon season, the first of the two peak spawning periods occurred outside the main typhoon season. The overall spawning period did not appear to correlate with any trend in inshore current speed, even though it occurred during the period when off-shore currents were strong. In general, the spawning timing of *A. vaigiensis* seems most likely to be associated with higher food availability for offspring. In addition, it seems quite possible that the timing of spawning may have been selected in order to retain larvae in their natal habitat.

Key words: *Abudefduf vaigiensis*, Environmental factors, Spawning season, Seasonal spawning, Sergeant major

Seasonal spawning has been observed in many reef fishes over a wide range of latitudes (Erdman, 1977; Russell *et al.*, 1977; Johannes, 1978; Walsh, 1987). For example, even though many fishes in the northeastern Caribbean spawn year-round,

they nevertheless show a seasonal peak once or twice per year (Munro *et al.*, 1977). Studies on the spawning patterns of reef fishes have also shown that in some demersal species there is a pronounced lunar periodicity of reproductive activity (Doherty, 1983; Foster, 1987).

1. Paper No. 368 of the Journal Series of the Institute of Zoology, Academia Sinica

2. To whom requests for reprints should be directed.

The adaptive significance of seasonal spawning provides valuable insight into the community ecology of coral reef fishes. If the fish community is structured by competition — as is assumed in resource-partitioning hypothesis (Mapstone and Fowler, 1986; Roberts, 1986) — it might be anticipated that a similar process would operate during the spawning season; indeed, the occurrence of spawning during a limited period might intensify competition between parents for reproductive resources, or between offspring for food resources. Also, the widespread occurrence of seasonal spawning suggests that the selective forces which account for this pattern are at least as important as the effects of competition.

Factors which may be responsible for the seasonality of spawning by reef fishes have been suggested over the last ten years. At the same time, various hypotheses have been proposed to account for the reproductive strategies of reef fishes (Johannes, 1978; Lowe-McConnell, 1979; Doherty, 1980; MacDonald, 1981; Thresher, 1984; Stanton, 1985; Robertson *et al.*, 1988). Most hypotheses assume that variation in environmental factors underlying the seasonality of spawning is predictable over time (Johannes, 1978; Barlow, 1981), and that the adopted strategy must normally maximize the survival of eggs and larvae subsequent to their release into plankton (Johannes, 1978; Doherty, 1980; Richards and Lindeman, 1987). These hypotheses have provided a framework — based on environmental factors such as temperature, tidal rhythms, currents, predator pressure on larvae, food availability, etc. — against which observations can be interpreted (Johannes, 1978; Lobel, 1978; Barlow, 1981; Doherty, 1983). However, as in most cases where observed patterns are most likely produced by unknown evolutionary mechanisms, testing of these hypotheses remains extremely difficult (Shapiro *et al.*, 1988).

In the present study we used the sergeant major damselfish, *Abudefduf vaigiensis*, to study the temporal pattern of its spawning activity in subtropical waters. We tested a variety of hypotheses by analyzing temporal variation in spawning intensity and its correlation with environmental factors. Subsequently, we drew conclusions regarding the possible adaptive significance of the reproductive strategy adopted by this fish.

MATERIALS AND METHODS

Study site

The present study was carried out in the subtidal zone at Kuei-hoe village (121°41'E, 25°12'N) on the northern coast of Taiwan (Fig. 1). The study site is located approximately 50 meters from the breakwater of the village's fishing port. Detailed descriptions of the study site were previously presented by Jan and Ormond (1992).

Fish

The sergeant major damselfish, *Abudefduf vaigiensis*, used in our study is abundant in the subtidal waters of northern Taiwan. Intermediate-sized sergeant majors forage on both algae and zooplankton (Jan and Chang, 1984; Sano *et al.*, 1984); however, larger individuals are more planktivorous than herbivorous (Fishelson, 1970; Jan and Chang, 1984).

Like other damselfishes, *A. vaigiensis* is a demersal spawner. Nests are formed by spawning males on the lateral surfaces of hard substrates, such as rocks or reefs (Jan, 1991; Jan and Ormond, 1992). After spawning, the male remains at the nest and assumes responsibility for egg-caring.

Study period

During the winter and early spring, northern Taiwan is affected by north-eastern

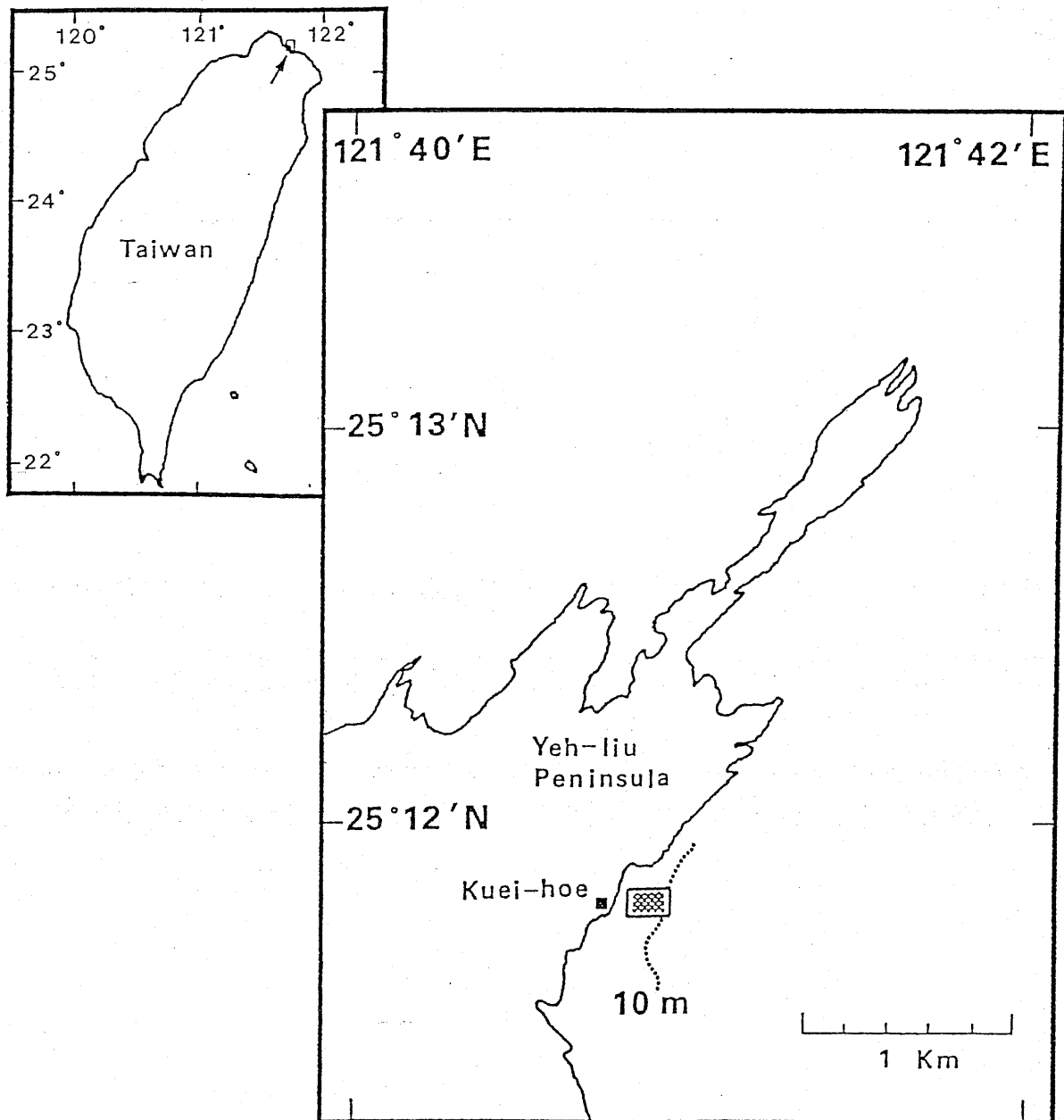


Fig. 1. Map of northern Taiwan showing location of study area. Note that the 10m isobath passes through the western part of the study area.

monsoon. During this period, diving is not possible due to rough seas. Eggs from *A. vaigiensis* clutches were inspected from April 17 to October 22, 1986. However, no data could be collected from June 13-23, when heavy rains caused high turbidity, and

August 24 - September 1, when typhoon Wayne prevailed.

Preliminary study

A preliminary study of the accuracy of our survey method was undertaken at the be-

ginning of the spawning period by comparing data collected by different numbers (one to four) of divers over two different observation periods. These tests were conducted under two separate conditions of underwater visibility; these were assessed as the maximum distance at which the shape of a 12cm white ball could be clearly identified.

On May 25, when underwater visibility was relatively poor (6m), a comparison of the numbers of nests located by four divers at two places (later designated as Sites A and B; see Fig. 2) showed that on average a single diver could locate 85% of possibly observed nests over a 30 min period. When observation time was extended for another 15 min (*i.e.*, to a total of 45 min), the percentage of nests located by one diver increased to 97%. The relationship between

the average percentage of nests located and the number of surveyors in this nest-survey is shown in Fig. 3A. On the other hand, data collected at three other sites (Sites C, D, and E) on May 27 (when underwater visibility was higher (13.5 m)) showed that a 25 min survey by one diver located 96% of the nests at any of these sites, while a 35 min survey located nearly all nests present (Fig. 3B).

Survey method

During the surveys the presence of nests was recorded; the ages of any eggs present were also estimated based on color and appearance (Jan, 1989). Subsequently, the number of nests found and the age of each nest were used to calculate the number of new batches of eggs spawned each day. In the data analysis, the number of new batches

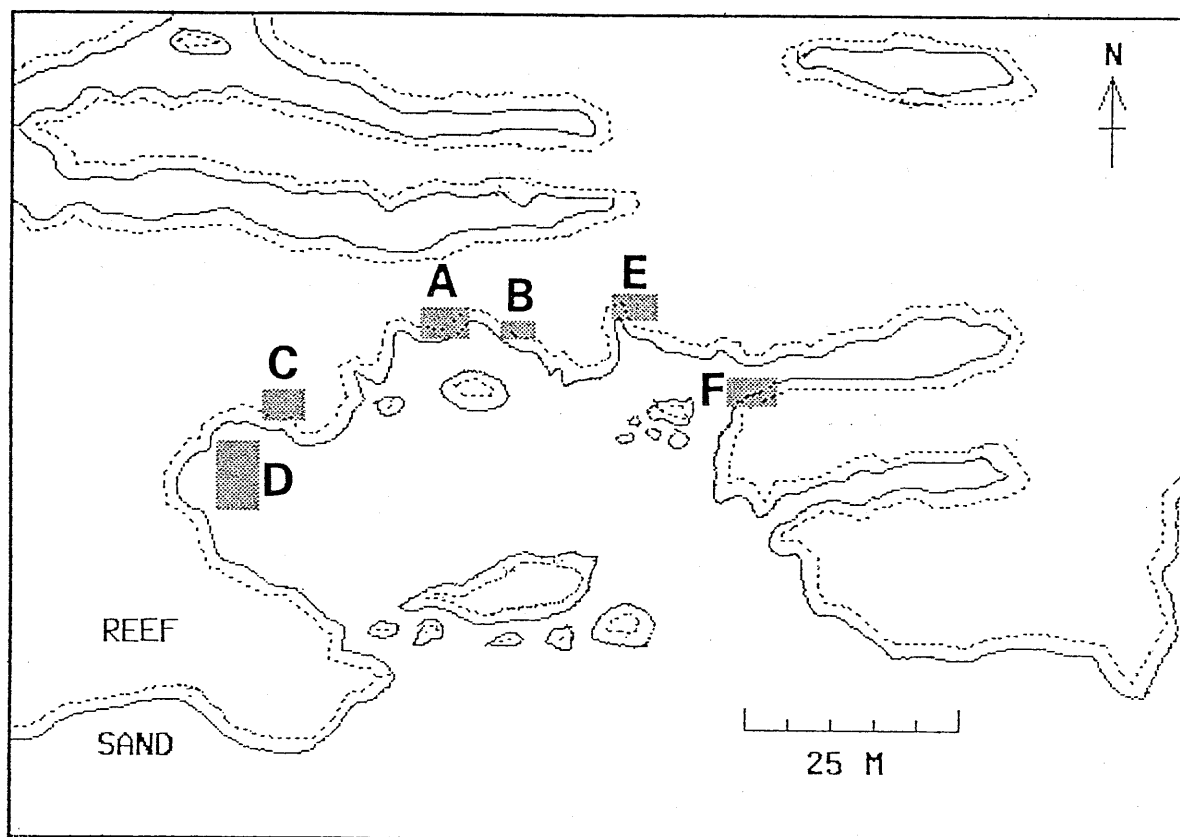


Fig. 2. Sketch map showing the distribution of spawning sites (hatched) of *A. vaigiensis* within the study area.

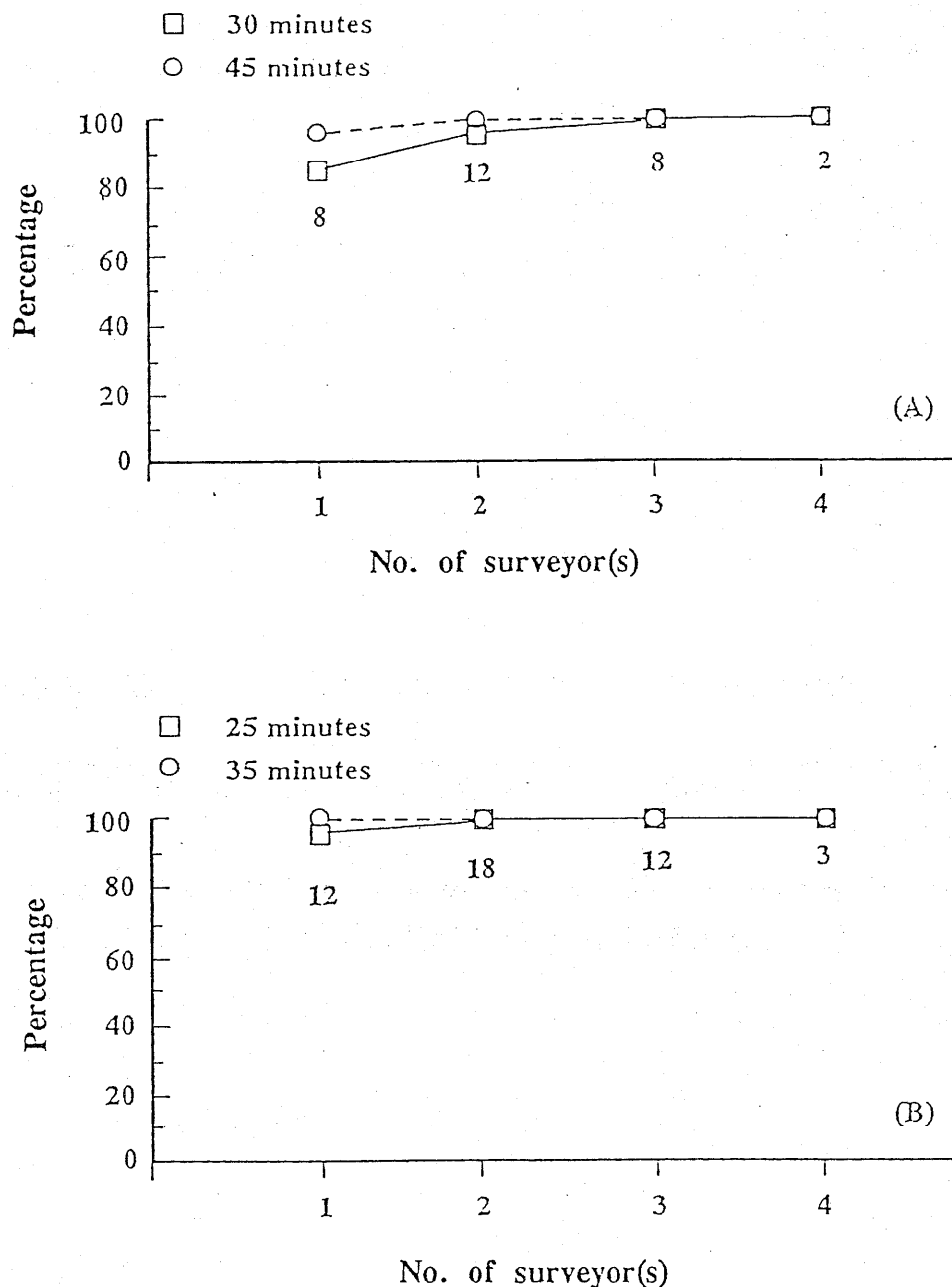


Fig. 3. Average percentage accuracy of locating nests by one to four surveyors over two different time periods. Graph A is based on nestcounts at two different spawning sites (Sites A and B) at a visibility of 6m; graph B is based on data collected at three sites (C, D and E) at a visibility of 13.5m. The label under each data point indicates sample size. Note that in Graph A, data for the 45 min period are composed of data obtained within the first 30 min period and data obtained within an extra 15 min period; the same is true for graph B.

of eggs is presented as *number of new nests*.

During the study period, underwater observations were undertaken at intervals

shorter than the hatching time of the eggs (*i.e.*, six days during May and five days during the following period); this was done to

ensure that no clutches were missed between observations. According to the results of the preliminary study, the number of divers and the survey time were adjusted to gain at least 95 percent accuracy. To eliminate, or at least to systematize sampling bias, bottom time was allocated according to underwater visibility. However, the efficiency of locating nests improved with experience. Hence, in the later period of this study, the time required for locating nests was considerably reduced.

Seawater temperatures were recorded from a wrist gauge to the nearest 0.5°C at a depth of 3m, or from a thermometer immersed in the same depth of water when diving was not possible.

DATA ANALYSIS

Assumptions

All data were analyzed based on two assumptions. First, all *Abudefduf vaigiensis* which spawned in the study area were assumed to be members of the same population. This assumption is supported by studies indicating that sergeant majors form separate local aggregations which are often associated with distinct sections of reef (Fishelson, 1970; Robertson, 1988). In addition, throughout the study period the spawning of *A. vaigiensis* was observed to be strongly associated with specific spawning sites, with some conspicuous individuals nesting at the same site during consecutive spawning periods. Thus, it is unlikely that these spawning sites were used in turn by different individuals from separate populations.

Our second assumption was that spawning did not occur during periods of disturbance caused by severe weather conditions such as heavy rains (*i.e.*, June 13-23) or typhoons (*i.e.*, August 24 - September 1). Heavy rains injected a large quantity of soil

into the coastal zone via nearby rivers. During this period, diving was only undertaken on June 17; even with the help of compasses and torches, observations were possible only at Sites A, B and E. No nests were found at these sites and it seems very unlikely that successful spawning could occur on parts of the reef where no observations were made. Similarly, the occurrence of typhoon Wayne during this study created difficulties; immediately after a previous typhoon we had observed that none of the nests formed just before the storm survived. Thus an assumption that no successful spawning could take place during a typhoon seems justified.

Spawning intensity

The number of newly formed nests was considered to be an indicator of spawning intensity, and this information was collected for different spawning sites over the entire spawning period. A quantitative expression of any trend in intensity was obtained by fitting a polynomial regression of the number of new nests (zeros being ignored) found daily at each spawning site as a function of time starting from May 1 — the date when the first new nests were found. The expression represented site-specific spawning intensity. However, because this method is not sensitive to any overall spawning periodicity, it cannot substitute for the periodicity test described below.

Spawning synchronization

To determine if the occurrence of synchronous spawnings at two or more spawning sites was statistically significant, we compared the number of days on which synchronous spawning occurred with the expected frequencies predicted; we did this based on the assumption that spawnings at each site were governed merely by site-specific probabilities. These probabilities were obtained by simply dividing the number of

days on which new nests were found by 169 — the number of days counted between the date on which the first nests were found and the date on which the last nests were found. The Chi-square was used to test for goodness of fit between the predicted and observed frequencies. In the test, the frequencies of spawning occurring synchronously at two and more than two sites were grouped to avoid violating the assumption of the normality of the data (Howell, 1985).

Spawning periodicity

The numbers of new nests found daily at different spawning sites were pooled over time for the entire spawning period in order to test whether spawning periodicity prevailed. This was tested both qualitatively and quantitatively. First, the binary sequence based on presence and absence of spawning was analyzed by a non-parametric method based on a *basic runs test* (Sokal and Rohlf, 1981) to determine whether spawning occurred randomly along the time axis. The null hypothesis suggests that the sequence is random, while the alternative hypothesis suggests the opposite, that is, the sequence has a tendency to cluster or intermix. Second, the randomness of the occurrence of daily numbers of new nests was examined by a *runs up and down test* to determine whether there are any long-term spawning cycles (Sokal and Rohlf, 1981). Furthermore, to reduce the risk of type II errors (Sokal and Rohlf, 1981) in the above tests, the daily data were pooled and tested against dates in the lunar cycle in order to check for any obvious lunar periodicity. If spawning followed lunar periodicity, then the sequence of the pooled number of new nests over the lunar cycle would not be random, since within the cycle one or more peaks in spawning would be expected to occur.

Environmental factors

In searching for any relationship between

spawning seasonality and environmental factors, information on monthly changes in those factors (including rainfall, typhoon occurrence, water temperature, salinity, zooplankton biomass, copepod abundance, and the strength of currents in local waters) were used. Except where otherwise mentioned, these data were collected from 1977-1985 at a station 15km to the west of the study area (Su *et al.*, 1978-1985).

In addition to water temperatures measured *in situ*, long-term data were also used to estimate yearly trends. The latter were also collected at a depth of 3m. Yearly trends were calculated according to Su *et al.* (1984b).

Data on zooplankton production was not available for the year the present study was undertaken. Instead, data from sampling conducted during the previous five years were used. Yearly trends in zooplankton biomass and copepod abundance were determined separately by fitting a polynomial regression to pooled annual data previously smoothed by Spencer's 21-term moving average smoother (Kendall, 1973). The abundance of copepods was considered separately, since copepods are known to be the major food of most marine fish larvae (Hunter, 1981).

Both the measured monthly rainfall for 1986 and rainfall averaged over past years were used. The mean rainfall for the period from January to June was based on data collected in the Taipei region from 1936-1984 (Liu, 1986), while that for July to December was based on data collected in the same region from 1946-1976 (Liang and Shen, 1987).

Information on typhoon prevalence from 1897-1984 was based on data published by Republic of China Central Weather Bureau (1986). The general features of seasonal variation in off-shore currents around Taiwan were based on Fan (1982). However, monthly variation in current velocity at three different water layers (upper, middle, and

bottom) in the inshore water column near northern Taiwan was also used (Liang *et al.*, 1981). These data were collected at two stations, at which bottom depths were either 120m or 122m, both stations are 30km to the north of the study area.

RESULTS

The first spawning was observed at Site A on May 1 (Fig. 2); a second spawning occurred at Sites C and D one week later. Mass spawning then commenced and lasted until late September. Apart from the three spawning sites mentioned above, there were three others (assigned as Sites B, E and F) within the study area (Fig. 2). Group spawning was characteristically observed for *A. vaigiensis*, but occasional solitary nests were also found. Most spawning sites were located on the edge of the reef framework, and were made conspicuous by aggregations of *A. vaigiensis* when spawning occurred. In early October spawning was only observed sporadically; our investigation continued until October 22, when conditions were again affected by the monsoon. The last egg batches were found on October 16 at Site F.

A total of 996 egg batches of *A. vaigiensis* was recorded over the entire season. Nests with egg batches occurred mainly at the above-mentioned six spawning sites (Sites A-F); those found away from these spawning sites were pooled and referred to as Site G. Results from further analyses are described below.

Spawning intensity

During the spawning period the spawning intensities of *A. vaigiensis* at five, of the seven spawning sites (A, C, D, E and G) decreased over time (Fig. 4). All spawning at these five sites showed a negative quadratic relationship to dates following 1 May. This indicates that the peak of spawning activity

occurred at the beginning of the spawning period. By contrast, at Sites B and F — where spawnings were interrupted for part of the spawning period — spawning intensities were not significantly correlated with time.

Spawning synchronization

Over the entire spawning period new nests occurred on a total of 58 days; on some of these days new nests were found at more than one spawning site. For example, as shown in Table 1, there were 15 days on which new nests occurred at two sites, 5 days at three sites, and one day at five sites. The expected frequencies, which were calculated based on the probability of spawning occurring at each spawning site, are also shown in Table 1. Test results show that the null hypothesis "spawning occurs independently at different spawning sites" can be decisively rejected at the 1% level ($X^2=10.21 > X^2_{.01}(2)=9.21$). In addition, our results show that the total number of spawning days observed (58) was much less than the number expected (70.2 days). These results indicate that spawning showed a tendency to occur synchronously at different spawning sites.

Spawning periodicity

Spawning occurred within the 169 day period. Results from the runs test on the presence and absence of spawning over the 169 days show that the null hypothesis (that spawning occurs randomly over the spawning period) should be rejected at the 0.1% level (Table 2). When the effects of severe physical disturbances (such as heavy rain and typhoons) were excluded by removing the appropriate dates from the time axis, the test indicated that the null-hypothesis should again be rejected, though at a lower significance level (5%) (Table 2). In other words, these results illustrate that spawning as a whole occurred in patches along the time

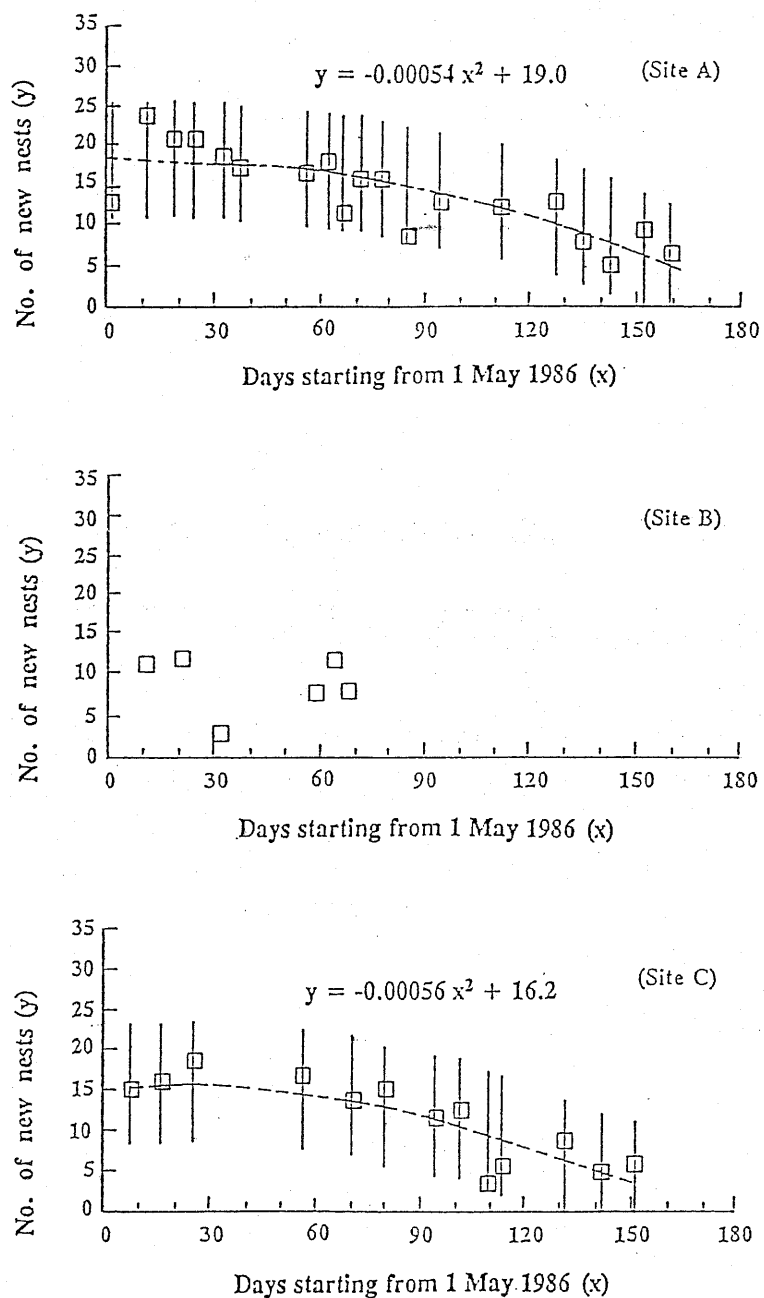


Fig. 4. Number of *A. vaigiensis* nests found daily at six main spawning sites (Sites A-F) and other locations (combined as Site G). Nil spawnings were ignored. When applicable, the spawning activity trend at each spawning site over time is indicated by a broken-curve with 95% confidence intervals (vertical lines) predicted for each data point. The fitted equation for each spawning site is shown next to the figure.

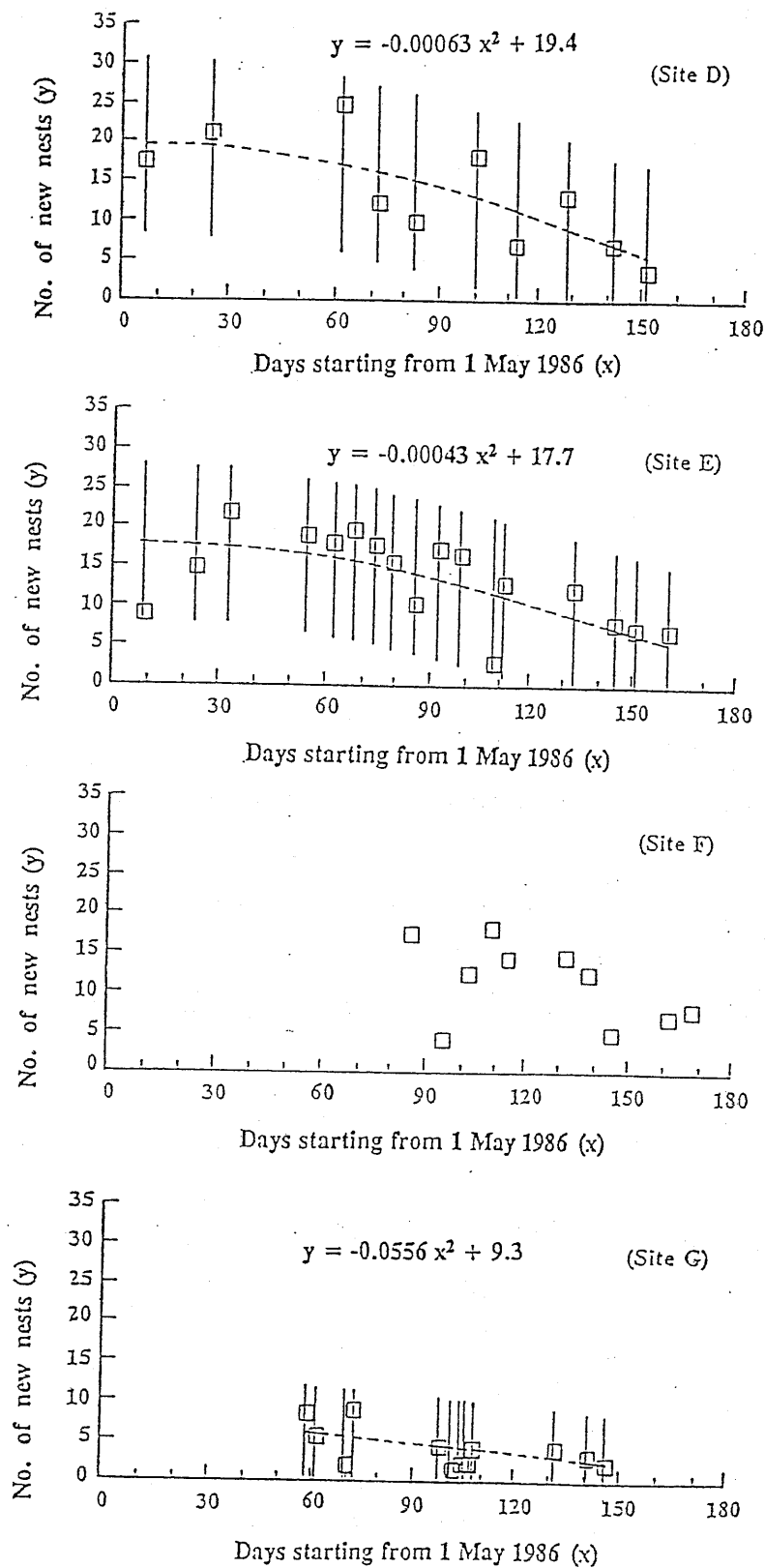


Fig. 4. (continued)

Table 1

Numbers of expected and observed days of synchronous spawning

Spawning occurred	Expected frequency (days)	Observed frequency (days)
(No spawning)	98.8	111
At 1 site	55.4	37
At 2 sites	13.0	15
At 3 sites	1.6	5
At 4 sites	0.1	0
At 5 sites	<0.1	1
At 6 sites	<0.1	0
At 7 sites	<0.1	0

axis.

The randomness of the sequential data for daily spawning strength, defined as the number of new nests found each day, was tested by the *runs up and down test*. In this test, the number of runs up and down was 64; the expected number was 56.3. The test statistic (t_s) is 1.86, which is above the 5% significance level ($t_s=1.96$). Accordingly, it is suggested that daily spawning strength occurred randomly, that is, there is no evidence showing that any long-term spawning periodicity exists.

The spawning period covered approximately six lunar months. When numbers of new nests found of *A. vaigiensis* were pooled against lunar cycle dates, we found that spawning occurred on 26 days of the lunar month (Fig. 5). The only two days on which no spawning occurred were before and after new moon. The results of runs tests show that the sequential occurrence of spawning during a lunar cycle followed a random pattern (Table 3). Moreover, though the daily number of new nests observed varied widely, average daily numbers for the period from full moon to new moon (exclusive) and the period from new moon to full moon (41 and 30, respectively) were not significantly different (Two-sample t -test

Table 2

Results of tests of runs for binary sequence of presence and absence of spawning during (a) spawning period, and (b) spawning period with dates of severe physical disturbance ignored.

	(a)	(b)
Days of spawning	58	58
Days of non-spawning	111	91
Number of runs	57	57
Expected number	77.2	71.9
t_s (large sample test statistic)	-3.37	-2.48
Probability (two-tailed)	<0.01	<0.05

$t=0.94$, $df=26$, $p=0.36$). There was, therefore, no indication of a significant lunar component in the spawning activity of *A. vaigiensis* in these waters.

Spawning seasonality and environmental factors

Temperature

At the beginning of May, when nests of *A. vaigiensis* were first found, water temperature measured *in situ* was 21.5°C. The temperature of the water increased from then on, reaching a peak of 28°C early in July. Thereafter, water temperature decreased gradually. At the end of the spawning period the water temperature was 24.5°C — still three degrees higher than the temperature at which spawning began.

Spawning was observed during a hypoth-ermal event (a temporary drop in water temperature) on May 24-26, with water temperature declining to 19°C, as well as in early July, when the water temperature reached its highest level.

Overall, the correlation between daily spawning intensity (assessed as number of new nests observed) and water temperature measured *in situ* was not significant (Fig. 6;

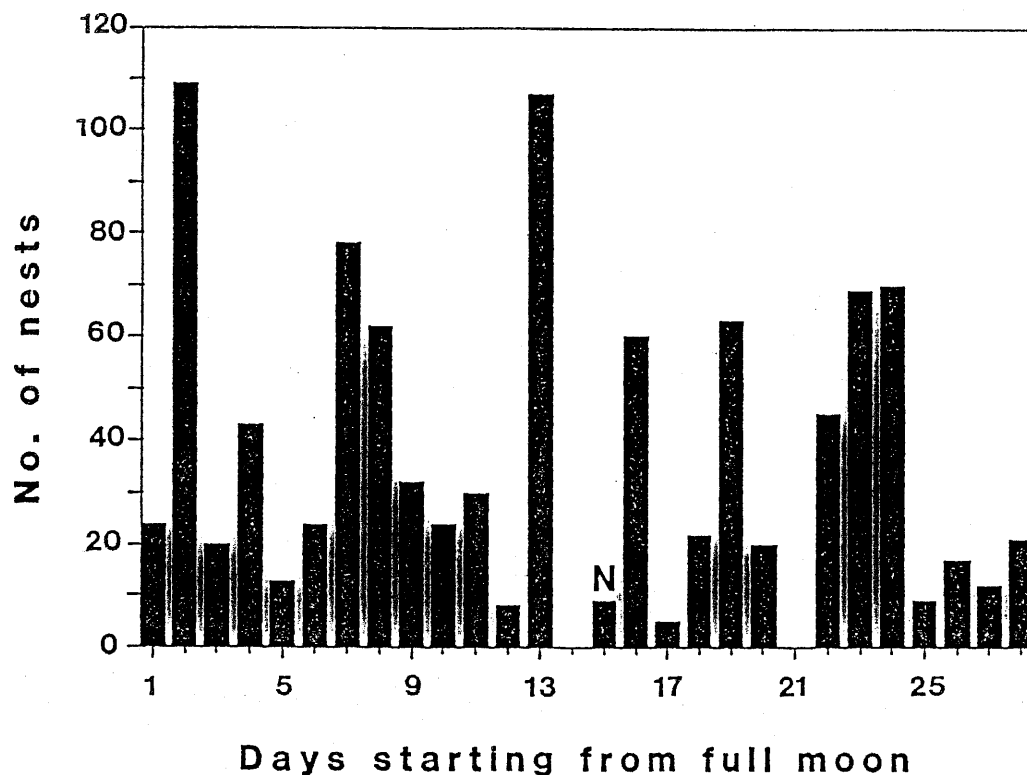


Fig. 5. Bar chart showing number of new nests pooled over the lunar cycle starting from full moon; N indicates the date of new moon.

Table 3

Results of tests for randomness of spawning over a lunar cycle starting from full moon.

Median = 24 (based on 28 observations)
 Number of runs above and below median = 14
 Expected number = 14.9286
 Large sample test statistic $t_s = -0.160$
 Two tailed probability $p = 0.87$

Number of runs up and down = 19
 Expected number = 18.33
 Large sample test statistic $t_s = 0.077$
 Two-tailed probability $p = 0.94$

t -test $df=56$ $p=0.93$). When compared with the annual temperature pattern estimated from seawater temperatures measured from 1977-1985 (Su *et al.*, 1978-1985), we found that spawning only occurred in the period when seawater temperature was relatively high (Fig. 7).

Zooplankton

Zooplankton biomass collected in 42 samples taken near the study area from 1977-1985 varied between 16-818 g/1,000m³ (Su *et al.*, 1978-1985). When the yearly total production trend of zooplankton was estimated, a yearly cycle with a summer peak was clearly shown (Fig. 8). The abundance of copepods — the major component of the zooplankton — varied in the range of 3,422-921,406 individuals/1,000m³, and also followed a similar annual trend (Fig. 8).

The spawning period of *A. vaigiensis* mainly overlaps the period of higher production of zooplankton. In our study, it commenced when production was expected to be increasing, persisted during the high production period, declined when production was predicted to be declining, and ceased when production was almost at its lowest.

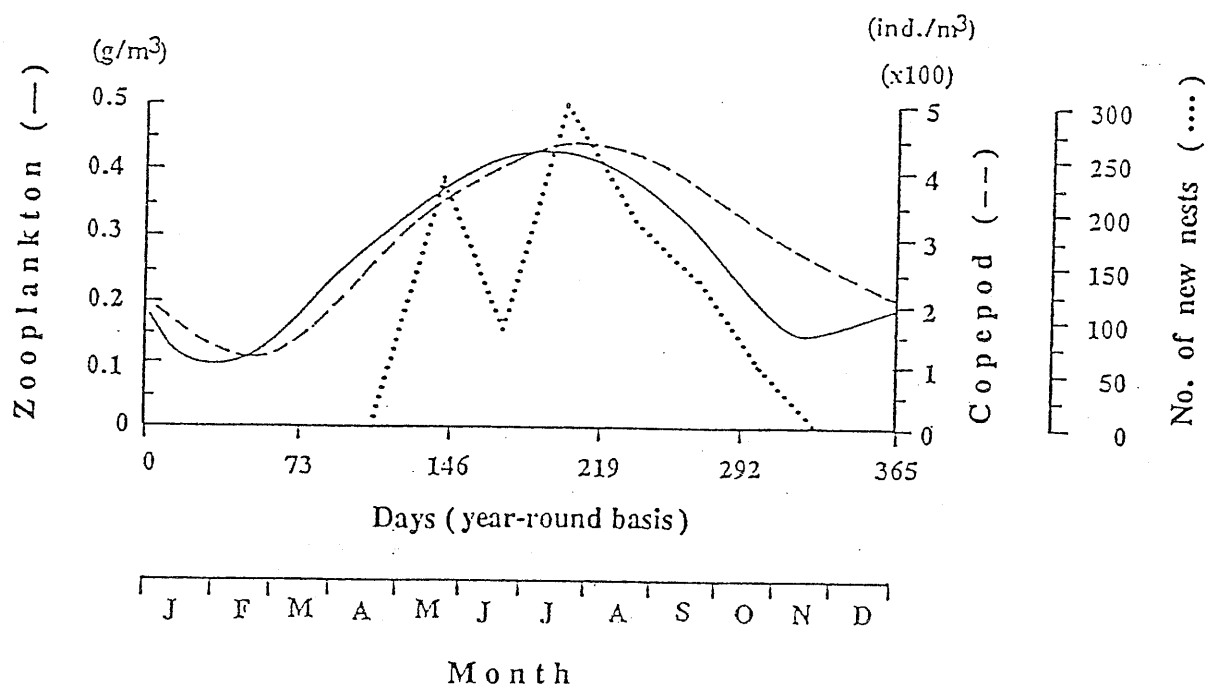


Fig. 8. Yearly zooplankton biomass and copepod abundance compared with monthly variation in the spawning activity of *A. vaigiensis*.

Rainfall and salinity

Rainfall in northern Taiwan is higher in summer; this was not only true in 1986, but has also been consistently true over the last 30 years (Liu, 1986; Liang and Shen, 1987). The amount of rainfall may contribute to the variation in salinity of coastal waters; salinity in local waters is lower in summer (Fig. 9). The spawning period of *A. vaigiensis* occurred in the period when rainfall was relatively high and salinity was low.

Prevalence of typhoons

There were 309 typhoons which affected Taiwan between 1897 and 1984 (Republic of China Central Weather Bureau, 1986). While almost all of these typhoons occurred during the period between April and November (Fig. 10), the period between July and September is the main typhoon season. The spawning period of *A. vaigiensis* occurs entirely within the typhoon period. Figure 10

shows that while the July spawning peak was inside the main typhoon season, the other peak spawning, which occurred in May, was outside the main typhoon season.

Current speeds

As explained above, the data on inshore current speed are averages of data collected at two inshore area stations during 1980-1981 (Liang *et al.*, 1981). Monthly variations in current speeds in the upper, middle, and bottom layers were not synchronous (Fig. 11). When taking mean current speeds in the three layers as a whole, no clear seasonal variation could be found. In addition, the spawning period of *A. vaigiensis* does not appear to correlate with any trend in inshore current speed. In contrast, off-shore currents in this region are stronger in summer (Fan, 1982). Thus, spawning appears to occur during period when the off-shore currents are strong.

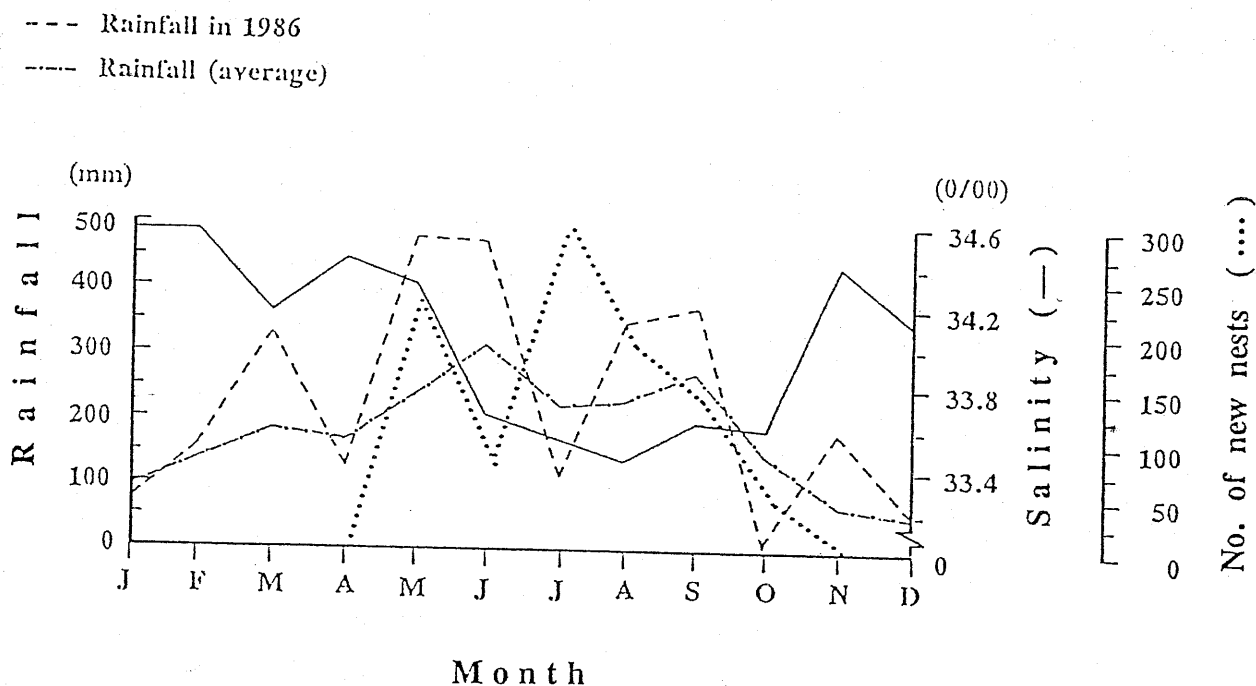


Fig. 9. Monthly variation in rainfall, sea water salinity, and spawning activity of *A. vaigiensis*.

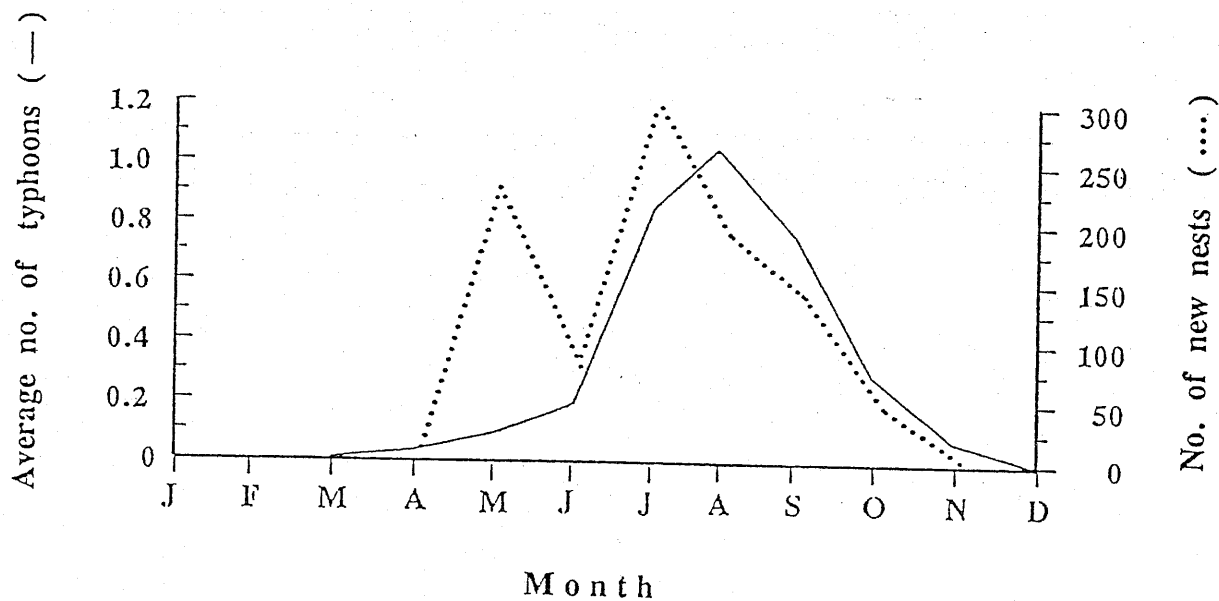


Fig. 10. Monthly variation in average occurrence of typhoons and spawning activity of *A. vaigiensis*.

DISCUSSION

The spawning of *Abudefduf vaigiensis* in the study area commenced in May and ceased in mid-October. Spawning tended to

occur synchronously at different sites, and did not follow any lunar periodicity. Although spawning in the same area is also known to have occurred in April (Jan and Chang, 1984), in our study no spawning was

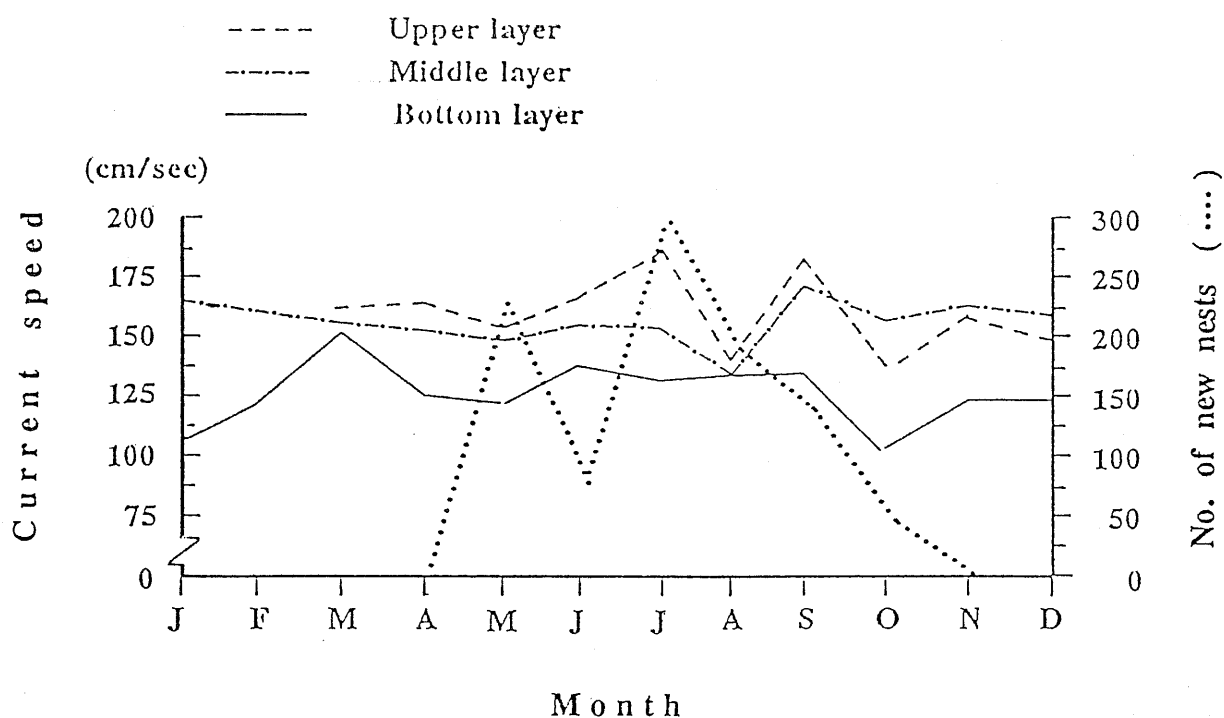


Fig. 11. Comparison of monthly variation in current speed in different columns of inshore waters and spawning activity of *A. vaigiensis*.

observed in late April. On the other hand, monthly underwater observations in relation to other projects were undertaken in the same area from 1979-1985 without any nests being seen during the winter periods (personal observations, RQJ). It is worth noting that in this study area the spawnings of other damselfish species also occurred within this period (Chang and Jan, 1983; Jan and Ormond 1992).

From an ecological point of view, it is meaningful to ask what is the adaptive significance for subtropical *A. vaigiensis* choosing to spawn during this period. A number of hypotheses have been proposed concerning the reproductive strategies of coral reef fishes. However, some of these hypotheses have been challenged for failing to accommodate proper tests (Shapiro *et al.*, 1988). Hence, before any hypothesis on factors underlying spawning seasonality can be accepted, it is essential to understand what benefit a fish spawning in one season might

gain over a fish spawning during another season.

In the tropics, some coral reef fishes spawn seasonally (Russell *et al.*, 1977); others spawn throughout considerable portions of the year, but also have peak spawning periods (Johannes, 1978; Sale, 1980; Walsh, 1987). A number of studies have suggested that spawning seasonality is correlated with the seasonal change in environmental factors — including temperature, day length (Walsh, 1987), rainfall (Foster, 1987), current velocity (Johannes, 1978; Williams *et al.*, 1984), and plankton productivity (Williams *et al.*, 1984). However, the adaptive significance of such a widespread pattern is still not clear. In contrast, in temperate regions — where marked seasonal fluctuations in environmental conditions are typical — a seasonal spawning pattern predominates. It has been suggested that this seasonal spawning in temperate regions has been adapted to ensure optimum conditions of day length, tempera-

ture, and food availability for developing larvae (Scott, 1979; Pitcher and Hart, 1982).

In our study area, environmental factors such as water temperature, abundance of plankton, local rainfall, physical disturbances, and velocity of off-shore current all vary seasonally. The spawning season of the observed sergeant majors occurred during the period of relatively high temperature, high production of copepods and other zooplankton, higher rainfall, strong off-shore currents, and lower disturbance by wave action — though with a higher degree of extreme physical disturbance due to typhoons. It seems that almost any of the environmental factors mentioned above can act as a cue for spawning. However, this may also cause other cues to be overlooked especially since seasonal variations of most of these environmental factors are interrelated. Therefore, it is much more revealing to consider each component separately.

Water temperature

Temperature is frequently cited as a potential controlling factor in the seasonal spawning of marine fishes (MacDonald, 1981; Stanton, 1985; Walsh, 1987). In the present study, the daily intensity of *A. vaigiensis* spawning was not significantly correlated to temperatures measured *in situ* (Fig. 6). Therefore, it is unlikely that temperature is the major factor controlling daily variation in the fish's spawning activity. However, there is a distinct summer/winter variation in water temperatures (Fig. 7), and the spawning season lies wholly within the period of relative high water temperatures; this suggests that the phasing of the reproductive cycle may be affected by seasonal changes in seawater temperature.

Food availability

Food availability is crucial for the first few weeks of larval life in marine fishes (Hunter, 1981). It has been widely observed

in mariculture that hatchlings and larvae are highly selective in choosing food resources (Chen, 1972; Liao *et al.*, 1972). Moreover, progressive starvation can decrease the larvae's searching and feeding abilities, consequently leading to a higher mortality rate (Houde, 1978; Hunter, 1981). Since, in seasonally variable environments, parental investment is expected to be allocated in accordance with environmental factors in order to maximize reproductive success (Dawkins and Carlisle, 1976; Carlisle, 1982), it seems reasonable to assume that fish are selected to spawn in periods when food availability for hatchlings is best assured (Cushing, 1977). This is supported by our results, which show a large overlap between the spawning season and the season of highest zooplankton production — including copepods, the most typical food source of most marine fish larvae (Fig. 8) (Hunter, 1981).

Currents and larval dispersal

There has been a vigorous controversy over whether the timing of spawning in reef fish is selected for maximum dispersal of hatchlings (Johannes, 1978; Lobel, 1978; Ross, 1978; Barlow, 1981; Doherty, 1983; Thresher and Brothers, 1985; Richards and Lindeman, 1987; Shapiro *et al.*, 1988). The probability of effective larval dispersal must, in theory, be linked to current strengths and directions at locations where larvae are released. In northern Taiwan the velocity of off-shore currents and wave height vary seasonally. The longshore current — which is dominated by Kuroshio, a warm ocean current from the tropics — prevails unidirectionally from south to north, and is relatively stronger during the summer (Fan, 1982). In contrast, in the outer inshore waters (bottom depth of more than 100m) monthly variations in current speed are evident (Fig. 11), though whether these variations follow any seasonal trends remains unknown. Closer to shore, in areas where the depth is less than

20m, the strength and direction of currents are profoundly affected by tides and underwater topography (Fan *et al.*, 1982; Hwung *et al.*, 1985). As a consequence, the strength and direction of inshore currents are more variable, and do not appear to follow the seasonal trends evident in the off-shore currents. Local wind speed and direction also vary seasonally; these variations contribute much to seasonal variations in wave height. As a result, wave height is greater in winter than in summer due to the prevailing north-eastern monsoon (Liang *et al.*, 1981); this contrasts with the strength of the off-shore currents.

A. vaigiensis spawning occurred in the period when the off-shore currents are relatively strong but the sea calmer; thus, it remains uncertain whether the studied fish has chosen to spawn at a time which favors maximal larval dispersal (Barlow, 1981), or one that favors better retention of larvae in their natal habitat (Johannes, 1978). *A. vaigiensis* spawning was mostly observed in the innermost area of a semi-enclosed bay. In view of the variation in inshore currents discussed above, there are doubts as to whether larvae produced in coastal waters could be successfully carried far enough to reach the off-shore currents. Instead, the larvae seemed more likely to be retained in the reef environment by water circulation affected by both the complexity of coastal topography and the semi-diurnal tidal rhythms. Moreover, since the spawning sites were close to shoreline (Fig. 2), the dispersal hypothesis prediction that free-ranging fish like the sergeant major will spawn at the edge of reef fronts in order to enhance larval drifting (MacDonald, 1981) is not supported either. In addition, our finding that the spawning of sergeant majors does not show any lunar periodicity also reduces the probability of the fish's using tidal currents to enhance larval dispersal. On the other hand, in these subtropical waters it would seem dis-

advantageous for parental fish to have their offspring carried northward by off-shore currents to areas where the water temperatures would normally be lower, since lower temperatures would presumably affect the survival of fish originating from coral reef areas.

Physical disturbance

In winter the sea is constantly affected by physical disturbances caused by the northeastern monsoon. Potts and McGuigan (1986) demonstrated that following gales, a population of postlarval goby, *Gobiussculus flavescens* almost completely disappeared from their former habitat. Therefore, it seems likely that a low survival rate of hatchlings can be expected if *A. vaigiensis* chose to spawn during the monsoon season. In contrast, if the fish choose to spawn in summer, then hatchlings face the risk of mortality due to typhoons (Lassig, 1983; Kaufman, 1983; Williams, 1984; Mah and Stern, 1986).

In our study area, two species of damselfishes (*Chromis fumea* and *Pomacentrus coelestis*) mostly spawn in May — when the sea is the calmest of the year (Jan and Ormond, 1992). The time lapses between the monsoon season, the spawning season of these two damselfish species, and the peak typhoon season (Fig. 10) make it possible to speculate that there may be a selective advantage in timing spawning activity so as to avoid catastrophic physical disturbances caused by monsoons and typhoons. While this may also explain the timing of the first spawning peak of *A. vaigiensis* observed in the present study, it fails to explain the occurrence of the second spawning peak in July — which is during the main typhoon season. Thus, even if the physical disturbance caused by a typhoon is a significant selective force on the reproductive strategies of these damselfishes, it is evidently either integrated with or overridden by other fac-

tors.

Synchronous spawning

When seasonal spawning is moulded by variation in a range of environmental factors on a broad scale, the adaptive significance of synchronous spawning at different sites is hard to assess.

The sergeant major *Abudefduf troschelii* has also been observed spawning intensively over a relatively short time period in the eastern Pacific (Foster, 1987). Foster suggested that the value of reproductive synchrony was as a mechanism for reducing predation on embryos through predation saturation (*i.e.*, predator swamping). However, the widespread occurrence of aggregate spawning by this damselfish (Albrecht, 1969; Cummings, 1968; Fishelson, 1970) has also been interpreted as suggesting that sexual selection and mate choice play an important role in the formation of spawning aggregations (Bradbury and Gibson, 1983).

A. vaigiensis lives in heterosexual social groups and exhibits multi-mate spawning. They spawn in leks — where each male defends an individual territory within a spawning aggregation (Loselle and Barlow, 1978; Thresher, 1984). Although the selective forces promoting lek spawning remain open to debate (Bradbury and Gibson, 1983; Jan, 1991), the synchronous spawning of *A. vaigiensis* at different sites is likely due to members of the same population having their spawnings governed by the identical cues. The dispersion of a population into several sub-leks may be the result of the nesting substrates for this damselfish being limited and distributed in patches throughout an area (Cummings, 1968; Albrecht, 1969; Gullion, 1976; Loiselle and Barlow, 1978; Jan, 1991; Jan and Ormond, 1992).

Overall, the timing of spawning the local fish — particularly when taking the damselfishes as a whole — seems most likely associated with higher food availability for

offspring. In addition, it seems quite possible that the timing of spawning may have been selected to retain larvae in their natal habitat. These factors (food availability and current speed) need not control gametogenesis directly, even though adjusting to these environmental influences may well be essential for successful reproduction; for example, gonad development and reproductive behavior might well be cued by seasonal changes in day length (Stacey, 1984).

This study was conducted in subtropical waters, and so the conclusions reached may differ from those based on data from the tropics. Further clarification of the reproductive strategies — including seasonal spawning — of reef fish may be advanced by similar studies conducted over a wider geographical range.

Acknowledgments: We would like to thank Dr. K.H. Chang for his lending of diving equipment and underwater photographic facilities and to Drs. Callum Roberts, Lynne Barratt, and Andrew Price for their invaluable comments on the manuscript. Field assistance in the preliminary study from F.K. Shiah, J.C. Chen, J.Y. Chiou, and M.S. Cheng is also appreciated. This study was supported financially by the R.O.C. National Science Council (partially through Project NSC81-0209-B001-01) and the Institute of Zoology, Academia Sinica, Republic of China.

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臺灣亞熱帶海域內條紋雀鯛的季節性生殖研究

詹榮桂 Rupert F.G. Ormond

本文係報導 1986 年 4 月到 10 月之間在臺灣北部礁岩海域潛水調查研究條紋雀鯛的生殖現象以及分析本種雀鯛的生殖強度與環境因子之間關係等所得的結果。條紋雀鯛的生殖出現於 5 月 1 日到 10 月 16 日之間，在總共 169 天的這一期間內，58 天裡有新的生殖巢出現，所記錄到的巢數共有 966 個。在此生殖期內有兩次生殖高峰(分列出現在 5 月和 7 月)；不過其生殖的發生並無明顯的月周期性。

生殖發生於較暖和的季節裡，但每天所出現的新生殖巢數與當天的水溫並無顯著的相關。雖然條紋雀鯛的生殖期落在颱風季節內，但第一個生殖高峰是在颱風盛行期之前。綜合此生殖季節內海域中動物性浮游生物的產量以及海流的強弱情形加以討論後顯示：條紋雀鯛很可能選擇在一個能提供其幼魚高食物來源的季節裡進行生殖；此外，選定這一生殖時間也有助於將仔魚保留在其出生地，而非令海流將仔魚帶到別處。

SHORT NOTE

THE DISCOVERY OF METAMORPHOSED JUVENILES OF FORMOSAN SALAMANDER (*HYNOBIUS FORMOSANUS*) IN YU-SHAN NATIONAL PARK

KUANG-YANG LUE and KUO-SHOU CHUANG

Department of Biology, National Taiwan Normal University, Taipei,
Taiwan 117, Republic of China

(Accepted March 3, 1992)

Kuang-Yang Lue and Kuo-Shou Chuang (1991) The discovery of metamorphosed juveniles of Formosan salamanders (*Hynobius formosanus*) in Yu-shan National Park. In March, 1991 the authors discovered two clutches of five and seven metamorphosed juveniles of *Hynobius formosanus* near the peak of Yu-Shan (Jade mountain), approximately 3,630m above sea level. The mean snout-vent length of these juveniles were 19.0 mm in nest one and 15.9 mm in nest two; larval survival rates were 35% and 48%, respectively. We estimated that the breeding season occurred from November to January.

Key-words: *Hynobius formosanus*, Metamorphosed juvenile, Clutch.

The Formosan salamander, *Hynobius formosanus*, is an amphibian species endemic to Taiwan; it occurs only in high mountain regions. In 1987, Chen and Lue reviewed its taxonomy, morphology, and distribution. Lue *et al.* (1989) and Yeh (1991) conducted ecological and population studies of *H. formosanus* in the Alishan area. Yeh *et al.* (1988) investigated its antipredator behavior. Clutch size and larval characteristics of this species were first reported by Kakegawa *et al.* (1989). However, no field record or data exists concerning the Formosan salamander. On March 28, 1991 the authors found two clutches of metamorphosed *H. formosanus* juveniles in Yu-shan National Park and made observations for the following report.

MATERIALS AND METHODS

Discovery sites were near the peak of

Yu-Shan, elevation of almost 3,600m above sea level. Morphological measurements were taken and are presented in Tables 1 and 2. The hatching rates of these two clutches were estimated based on clutch sizes reported by Kakegawa *et al.* (1989). In addition, collections of *Ambystoma californiensis*, *Onychodactylus fisheri*, *Hynobius retardatus*, *H. peropus*, and *H. tsuensis* from the California Academy of Science were checked for comparison.

RESULTS AND DISCUSSION

Both broods were found under stones at sites where the ambient temperature was 8°C. The altitudes of the two sites were 3,625m and 3,630m above sea level. Vegetation type in the surrounding area is alpine grassland dominated by *Yuahania niitakayamensis* and *Juniperus squamata*. On the day of discovery, the snow on the ground was melting and seeping into the mountain